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Geographic variation in *Lycaena xanthoides*

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Abstract.—Fifteen wing characters analyzed from seven populations, and larval foodplant information, are used to correct an error in the systematics of the *Lycaena xanthoides* group. *L. x. xanthoides* and *L. x. editha*, formerly considered separate species, are closely related and connected by intermediate populations. *L. x. dione,* previously considered conspecific with *L. xanthoides*, is the most distinct entity. These allopatric subspecies form a cline from *L. x. dione* to *L. x. xanthoides* to several populations in California intermediate between *L. x. xanthoides* and *x. editha* to *x. editha* from California-Oregon to *x. editha* from the Rocky Mountains. The major gap in the cline is between *x. dione* and *x. xanthoides.* The cline is horseshoe-shaped, with the most distinct entities parapatric (but altitudinally separated) along the eastern edge of the Rocky Mountains.

Introduction

In 1974 I collected a series of *Lycaena* from northern California which seemed intermediate between *xanthoides xanthoides* and *x. editha.* In attempting to place this series I found that an error has been perpetuated in the systematics of the group. I will attempt to show that *xanthoides* and *x. editha*, previously considered separate species, are closely related and connected by intermediate populations, and that *x. dione,* previously treated as a subspecies of *xanthoides,* is much more distantly related.

Characters studied include male and female genitalia, the eleven wing pattern characters listed and described in the explanation for Fig. 1, the position of the submarginal brown spot in cell $Sc+R_1$ on ventral hindwing, forewing shape, and the uniformity (solid versus lighter centers) of ventral hindwing median and basal spots.

Results

Genitalia. 54 dissections of male and female genitalia were made of all entities of the group, but the only difference found was a general increase in robustness of genitalia as size increases from *"montana"* to *editha* to intermediate populations to *xanthoides* to *dione.* Valvae and sterigmae are too variable individually to detect differences, and the valval process usually differs as much between right and left valvae as between individuals.

Wing pattern. Fig. 1 plots most wing characters. The *x. dione, x. editha,* and *x. "montana"* samples are from several locations each, which were combined in Fig. 1 when found to have the same wing pattern.

The series from Dunsmuir in northern California is intermediate between *x. editha* and *x. xanthoides* in every trait by which the two are distinguished: in wing length, in size of ventral hindwing spots, and in thickness of submarginal white band on ventral hindwing (this character is of little value because it varies somewhat between *x. xanthoides* populations). The Dunsmuir series has a slightly less well developed red marginal band on dorsal hindwing, a character which does not differ appreciably between *x. editha* and *x. xanthoides.*

The series from near Mather on the western slope of the Sierra Nevada in central California, is also intermediate between *x. xanthoides* and *x. editha* (Fig. 1). It is intermediate in wing length, and is also intermediate in ventral hindwing postmedian spot size except that the maritime Point Richmond *x. xanthoides* population approaches it in spot size. The submarginal white band on ventral hindwing is thicker than in most *x. xanthoides* populations. The smallest and most heavily spotted male from near Mather (collected September 4) was reported as *editha* by Shields (1966), who reported the other intermediate specimens (collected 24 June to 1 August) as *xanthoides.* The very late September date of the former specimen may mean that it flew down from higher altitude in Yosemite Park to the east, where numerous *x. editha* populations occur.

The previous classification, which grouped *x. xanthoides* and *x. dione* into *xanthoides,* and *x. editha* and *x. "montana"* into another species *(editha),* is wrong because *x. editha* and *x. xanthoides* are much more similar to each other than either is to *x. dione. L. x. xanthoides* and *x. editha* differ basically by only two characters. *L. x. dione* differs from *x. editha* and *x. xanthoides* in eight characters: it 1) has more black spots on margin of ventral hindwing, 2) has more red lunules there, 3) has more red lunules on margin of ventral forewing, 4) has the red band on margin of dorsal hindwing slightly better developed and thicker, 5) and has a whiter ground color of ventral hind wing. 6) The submarginal ventral hindwing brown spot in cell $Sc+R_1$ seems to be closer to wing base than the same spot in cell Rs in *x. dione,* but is usually equal to or farther from base in *x. xanthoides* and *x. editha.* 7) The ventral hind wing median and basal spots have lighter centers in *x. xanthoides* and *x. editha,* but are solid black in *x. dione.* 8) The male forewings seem more rounded in *dione* than in the others.

L. x. "montana" differs slightly from *x. editha* in having slightly smaller wing length, slightly larger ventral postmedian spots, slightly fewer black spots and red lunules on margin on ventral hindwing, and slightly greater extent of red on margin of dorsal fore- (females) and hindwing and of orangish flush on female dorsal forewing.

The three *x. xanthoides* samples differ somewhat from each other. The Point Richmond sample was collected within 100 meters of the sea of San Francisco Bay, and differs in several traits from inland samples: it is somewhat larger, has slightly larger postmedian spots on ventral hindwing, has a somewhat thinner white submarginal band on ventral hindwing (like *x. dione*), has a somewhat browner ventral ground color, and has slightly greater orange flush on ventral forewing. It is slightly more similar to *x. editha* than are the other two *x. xanthoides* samples. The few inland northern California samples examined appear more similar to southern California populations.

Except for local trends, the geographic variation within this group shows a cline from *x. "montana"*, to *x. editha,* to the California populations intermediate between *x. editha* and *x. xanthoides,* to *x. xanthoides,* and finally to *x. dione.* A roughly clinal pattern is shown by these characters: wing length, width of postmedian-median ventral hindwing spots, number of red lunules and width of white band on ventral hindwing margin, color of ventral hindwing, and number of red lunules on margin of ventral forewing. The two most different members are *x. "montana"* and *x. dione,* and the major gap in the cline is that between *x. xanthoides* and *x. dione. L. x. xanthoides* and *x. dione* are separated by almost 2000 km at present, although I think that in Pleistocene or earlier time intermediate populations probably occupied Arizona, New Mexico, or Mexico. The cline is therefore horseshoe-shaped, and the two endpoints are now parapatric but altitudinally separated from Colorado to Montana.

Distribution (county records only for the U.S.) *L. x. editha.* ALBERTA: southern foothills, Calgary-McLeod area; COLORADO: Moffat, Routt, Grand, Gilpin, Jackson, Larimer; WYOMING: Sheridan, Park, Bighorn, Johnson, Teton, Sublette, Fremont, Lincoln, Converse, Platte, Albany, Yellowstone Nat. Park; MONTANA: Ravalli, Flathead, Missoula, Granite, Lewis & Clark, Cascade, Chouteau, Jefferson, Gallatin, Sweetgrass, Beaverhead, Madison, Carbon, Lake, Stillwater, Mineral, Broadwater; IDAHO: Clearwater, Shoshone, Adams, Latah, Idaho, Lemhi, Fremont, Custer, Clark, Bear Lake, Valley, Boise, Ada, Elmore, Blaine, Cassia; UTAH: Salt Lake, Summit, Cache, Rich; NEVADA: Elko, Washoe, Storey, Ormsby; WASHINGTON: Walla Walla, Columbia; OREGON: Klamath, Morrow, Crook, Umatilla, Wallowa, Union, Baker, Wheeler, Grant, Lake, Lane, Harney, Jackson; CALIFORNIA: Siskiyou, Shasta, Plumas, Sierra, Tehama, Tuolumne, Madera, Inyo, Alpine, Nevada, Placer, Mariposa, Modoc, Mono, Tulare.

L. x. xanthoides. OREGON: Benton, Jackson, Yamhill; CALIFORNIA: San Diego, Los Angeles, Kern, Inyo, Riverside, Mendocino, Orange, Monterey, Tulare, Contra Costa, Lake, Marin, Stainislaus, Santa Clara, Alameda, Tuolumne, Sonoma, Solano, San Mateo. BAJA CALIFORNIA NORTE: just south of Calif.

L. x. dione. COLORADO: Larimer, Weld, Morgan, Logan, Sedgwick, Phillips, Yuma, Boulder, Jefferson, Denver, Adams, Arapahoe, Douglas, Elbert, El Paso, Fremont, Pueblo, Kit Carson, Bent, Prowers; WYOMING: Campbell, Bighorn, Sheridan, Johnson, Crook, Converse, Platte, Albany; MONTANA: Glacier, Prairie, Custer, Lewis & Clark, Sweetgrass, Cascade, Chouteau, Stillwater, Carbon; NORTH DAKOTA: Bottineau, Cass, Grand Forks, McKenzie, Pembina, Slope; SOUTH DAKOTA: Lawrence, Codington, Harding, (Marshall or Roberts); NEBRASKA: Dawes, Sheridan, Deuel, Platte, Dodge, Kearney, Adams, Fillmore, Douglas, Saunders, Seward, Lancaster, Nuckolls, Thayer, Jefferson, Gage, Johnson, Nemaha, Pawnee, Richardson, Saunders; KANSAS: Scott, Riley, Johnson, Pottawatomie, Greenwood, Douglas, Franklin, Marion; OKLAHOMA: Rogers, Cleveland, Craig; MISSOURI: Jasper, Randolph, Johnson, Cass, St. Clair, Clay, Morgan, Carroll, Livingston, Lafayette, Buchanan, Saline, Jackson, St. Charles, Holt, Vernon; IOWA: Guthrie, Story, Linn, Pottawattamie, Johnson, Woodbury, Winneshiek; MINNESOTA: Hennepin, Rock, Houston, Wabasha, Polk, Aitken, Big Stone, Winona, Pipestone, Redwood, Goodhue, Scott, Dakota, Lac Qui Parle, Kanabec, Clay, Lake, Sherburne, Carlton; WISCONSIN: Grant, Eau Claire, Milwaukee, Marquette, Burnett, Dane, Door, Pepin, Chippewa, St. Croix; ILLINOIS: Mercer, Madison, Henderson, McDonough, Pike, McLean, LaSalle, Kane, Lake, Cook, DuPage, Grundy, Putnam, Marshall, Peoria, Livingston, Ford, Champaign, Shelby, Cass; MANITOBA: Victoria Beach, Winnipeg, Silver Height, Brandon, Housavick, Rosebank, Beulah, Birtle, Miniota, near Transcona; SASKATCHEWAN: Punnichy, Saskatoon, Lloydiminster, Tantallon, Fort Qu'Appelle; ALBERTA: Johnson Creek near Plateau Mtn., vic. Medicine Hat, Lethbridge, Calgary, Wainwright, Edmonton, Crows Nest Pass, Tilley, head of Pine Creek, Waterton area.

Interdigitation of ranges. L. x. editha occurs at higher altitude than *x. xanthoides* and *x. dione,* so that in some cases *x. editha* and one of the other subspecies occur near each other in mountains versus lowlands. *L. x. editha* and *x. dione* occur in the same county in Montana (2 counties), Wyoming (5 counties), and Colorado (1 co.), but never occur together at the same locality, because of altitudinal separation. *L. x. xanthoides* and *L. x. editha* are also altitudinally separated where their ranges interdigitate in southern Oregon and California (both occur in Jackson Co. Ore.). In northern California *x. xanthoides* occurs below 1000', whereas in the southern Sierra Nevada it occurs at higher altitudes.

Immatures. No differences between the species other than size have been found among eggs, larvae, or pupae as yet. *L. x. dione* eggs are larger with coarser sculpturing than eggs of *x. editha.* Comstock & Dammers (1935) found that *x. xanthoides* larvae are quite variable in

color, and Skinner (1893) found no obvious difference between larvae of *x. dione* and *L. hyllus* (Cramer).

Hostplants. It has been thought that *x. xanthoides* larvae eat *Rumex,* whereas *x. editha* larvae eat *Potentilla.* However, the *Potentilla* records for *x. editha* are dubious; it also eats *Rumex. L. x. xanthoides* hosts include *Rumex hymenosepalus* (Comstock & Dammers 1935), *Rumex* sp. (Scott & Opler 1974, reported erroneously as *R. hymenosepalus*), *R. pulcher* (Emmel & Emmel 1973), *R. crispus* and *R. californicus* (both larvae reared, Idyllwild, Riverside Co. Calif., John F. Emmel, pers. comm.), and both *R. crispus* and *R. conglomeratus* (Shapiro 1974). *Hemizonia* sp. (Tietz 1972) is an error because it is not listed in either of te sources Tietz cites. *L. x. dione* hosts include *Rumex obtusifolius* (Forbes 1960; Leussler 1938-1939), *R. salicifolius triangulivalvis* (ovipositions Red Rocks, Jefferson Co. Colo., 12 July 1973, J. Scott), *R. occidentalis* (oviposition 2 mi. N. Idledale, Jefferson Co. Colo., 1977, J. Scott), *R. crispus* (oviposition 2 mi. N. Idledale, 1977, J. Scott), *R. "longifolius"* (Skinner 1893; Tietz 1972 cites this record under the name *R. occidentalis*), and "blunt-leaved dock" (Hooper 1973). *L. x. editha* hosts include *Rumex acetosella* (ovipositions Toll Ranch, Gilpin Co. Colorado, 27 July 1977, J. Scott; oviposition Jim Creek, Grand Co. Colo., 9 August 1977, J. Scott; oviposition California, Emmel & Emmel 1974), *R. gracilescens* (Tilden 1959), *R. paucifolius* (Garth & Tilden 1963), *Polygonum phytolaccoides* (oviposition Donner Pass, California, A. Shapiro pers. comm.). Both *Rumex* and *Polygonum* are Polygonaceae. Records of *Potentilla (Horkelia) fusca* (oviposition on leaves, Lembert 1894) and *Potentilla tenuiloba* (Comstock 1927) are old and somewhat dubious in view of the behavior of females in crawling down a hostplant stem and laying eggs haphazardly on or near stems or trash nearby.

Discussion

I treat *L. x. xanthoides* and *x. editha* as conspecific because: 1) they differ only by two wing characters (one or both of which might be influenced by temperature); 2) the Dunsmuir and Mather populations which are intermediate, indicating the probability of gene flow between the two; and 3) they both use Polygonaceae as larval hosts. *L. x. dione* could be considered a separate species because it is the most distinct entity, but I treat it as a subspecies of *xanthoides* because previous authors have done so (Clench 1961) and because it forms one end of a cline involving the other entities. The Rocky Mountain *x. "montana"* differs slightly from *x. editha* as noted above, and forms the other end of the cline. Because *"montana"* is less distinct than the other three

entities I prefer to treat it as a synonym until more complete studies of geographic variation are made of *L. x. xanthoides* and *x. editha.* Some persons may wish to consider *"montana"* a valid subspecies. *L. x. "luctuosa"* Wats. & W. P. Comstock, named from Tehachapi, California, I treat as a synonym of *xanthoides* for the same reason. The name *luctuosa* may be useful when the geographic variation within *x. xanthoides* is better studied and a specific type locality for *xanthoides* is designated. The following treatment is suggested.

L. xanthoides
- a. *x. dione* Scudder 1868
- b. *x. xanthoides* (Boisduval) 1852
  luctuosa (Watson & W. P. Comstock) 1920
- c. *x. editha* (Mead) 1878
  montona Field 1936

It would be of great interest to know the effect of temperature on the wing pattern of *xanthoides.* The smaller and more heavily spotted *x. editha* might result partly from its higher altitude environment when compared to lowland *x. xanthoides.* The maritime Point Richmond *x. xanthoides* might be influenced by climate as well. Other California butterflies such as *Phyciodes campestris* are known to differ with altitude in part due to environmental causes (A. Shapiro pers. comm.).

It is of interest that Johnson & Balogh (1977) in describing *L. rubidus ferrisi* as a distinct species, justified this in part by stating that the differences between *L. rubidus* (Behr) and *L. r. ferrisi* are as great as those between *x. xanthoides* and *x. editha.* This paper shows that the comparison can no longer be used as justification. I dissected a series of *r. ferrisi* collected by Kilian Roever and found very little difference between it and *rubidus* (or *xanthoides*) in either male or female genitalia. The valvae are variable and very similar although *r. ferrisi* has slightly shorter valvae which can be seen only by using measurements or by placing the two side-by-side. Several wing pattern differences were noted, although one *r. ferrisi* lacks the ventral forewing orange flush considered diagnostic, and other *r. ferrisi* have the wing shape of *rubidus* rather than the shorter wing shape considered diagnostic of *r. ferrisi.*

Three apparent interspecific hybrid *Lycaena* were found during this study and indicate that mating occurs successfully between entities more different than are the subspecies of *xanthoides* or *rubidus.* David Wagner caught an apparent F_1 hybrid between *L. x. dione* and *L. rubidus* in the foothills west of Fort Collins, Larimer Co. Colorado. Marc Epstein caught an apparent F_1 hybrid between *L. x. editha* and

L. rubidus at Rabbit Ears Pass, Routt Co. Colorado. The Los Angeles County Museum has a female from Castella, Shasta Co. California, July 1903 (J. A. Comstock collection) in which the underside resembles a very heavily marked *L. heteronea gravenotata* Klots but the upperside resembles a partly orange female *L. rubidus* (*heteronea* females lack orange). Considering that *rubidus* does not occur in the area (except for one dubious specimen labeled "Mt. Shasta"), and that *heteronea* occurs there only as ssp. *L. h. heteronea* Boisduval, it probably represents a hybrid between *L. h. heteronea* and another *Lycaena,* possibly an *L. xanthoides* intermediate population like at Dunsmuir only a few km to the north, or *L. nivalis* (Boisduval).

One female from Point Richmond has 6 large submarginal blue spots on each wing. This is significant in showing that the ability to produce blue (which reflects ultraviolet) is present in the gene pool of this species, which is otherwise nonreflective in uv. Ultraviolet reflection is frequent in other *Lycaena* (Scott 1973). Orange flush on ventral forewing was not found in *x. dione* in this study although Clench (1961) states that occasional individuals have it.

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Appendix

Localities and Characters Studied: The sample of *x. dione* is from Colorado (21), Iowa (3), Alberta (1), Missouri (6, coll. R. Heitzman); others from Colorado (60) and Iowa (1) were examined but not included in Fig. 1. *L. x. xanthoides* are from San Diego Co. California (29, coll. O. Shields and R. Breedlove), near Techachapi, Kern Co. California (2), Glacier Lodge, Inyo Co. Calif. (1, coll. C. L. Hogue), Havilah, Kern Co. Calif. (1, coll. O. E. Sette), Greenhorn Mts., Kern Co. Calif. (2, M. L. Walton), Big Pine Meadow, Tulare Co. California (15), Point Richmond, Contra Costa Co. Calif. (28). Others from northern California (12) and Point Richmond (114) were examined but not included in Fig. 1. *L. x. xanthoides-editha* intermediates are from Railroad Park, 2250 ft., Dunsmuir, Siskiyou Co. California, 23 June 1974 (17), and from the vicinity of Mather (most 1 mi. east), Tuolumne Co. Calif. (20, coll. O. Shields), about 4600 ft. *L. x. editha* from Klamath Co. Ore. (5), Siskiyou Co. Calif. (4), Shasta Co. Calif. (9), Plumas Co. Calif. (9), Sierra Co. Calif. (1), Tehama Co. Calif. (1), Tuolumne Co. Caif. (2), Madera Co. Calif. (3), all coll. by O. Shields, D. Dirks, T. Preston Webster. 148 others from Inyo, Placer, Modoc, Tehama, Siskiyou, Shasta, Mono, Alpine, Tuolumne, and Nevada Cos. California, and Wallowa, Crook, and Klamath Cos. Oregon, were examined but not included in Fig. 1. *L. x. "montana"* are from Ravalli Co. Mont. (7), Cascade Co. Mont. (4), Sheridan Co. Wyo. (3), Yellowstone Park Wyo. (3), Moffat Co. Colo. (4), Routt Co. Colo (1), Grand Co. Colo (14), Gilpin Co. Colo. (13). Most were collected by myself unless otherwise noted. Some are from the Los Angeles County Museum.

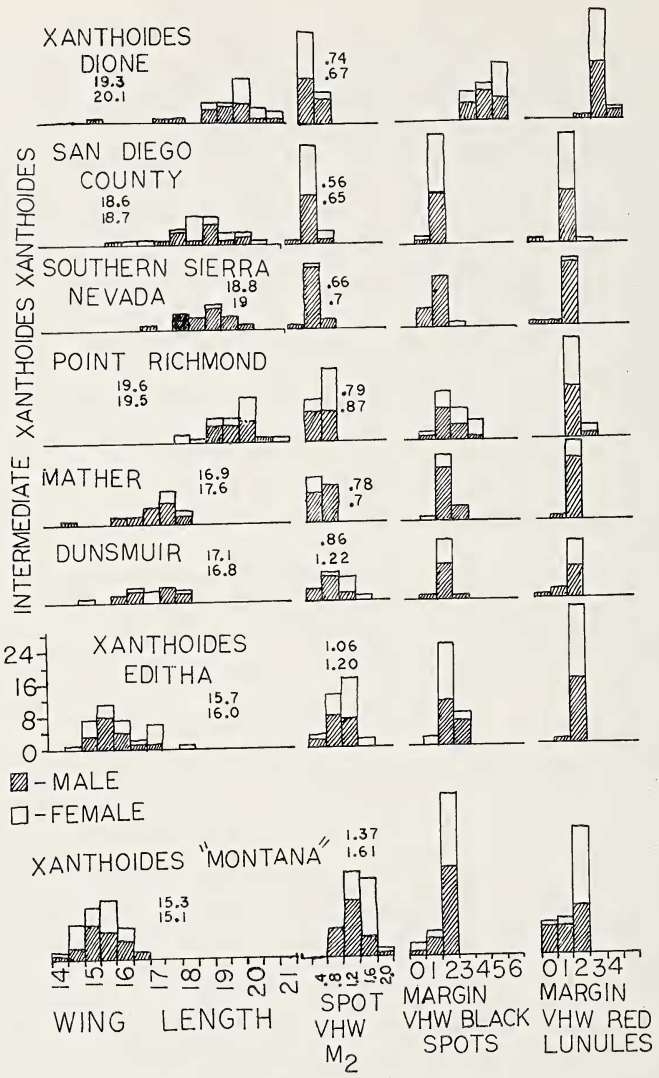
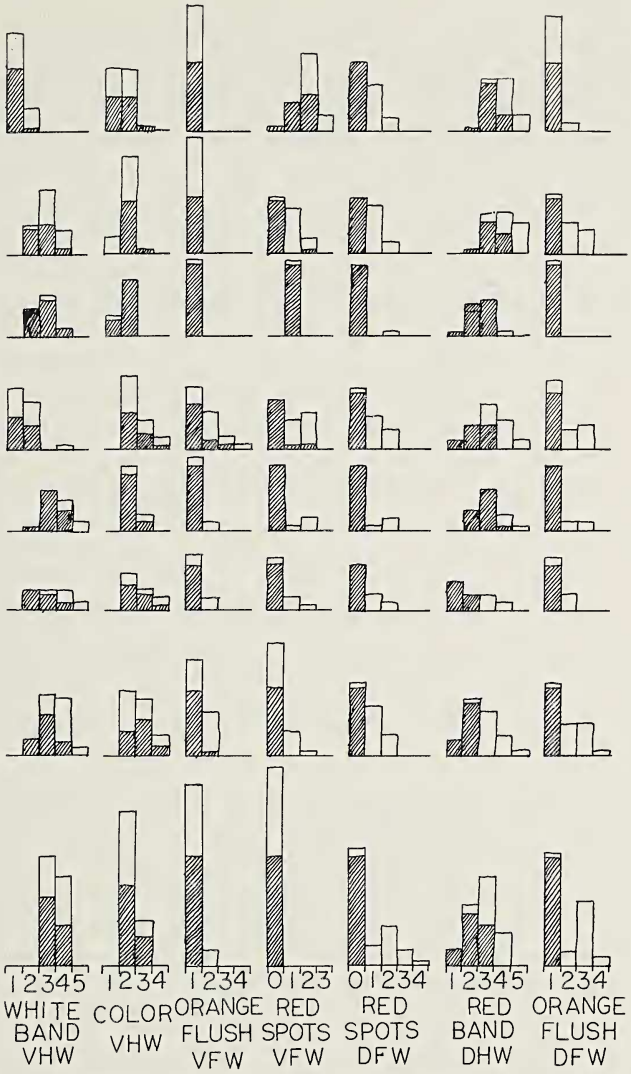


Fig. 1 Histograms showing the number of individuals of each sex which have each character state. Character states are (characters from left to right): 1) length of right forewing (mm); 2) width (mm) parallel to wing veins of ventral hindwing postmedian brown spot in cell M_2 (in intervals of .4 mm starting with 0, .4, .8, 1.2, 1.6, 2.0); 3) number of spots on margin of ventral hindwing which are black rather than brown (from 0 to 6); 4) number of red lunules on margin of ventral hindwing (from 0 to 5); 5) thickness of submarginal white band capping the marginal spots on ventral hindwing (1-very thin, about .3 mm thick; 2-thin, about .5 mm thick; 3-thicker, about .8 mm thick; 4-thick, about 1.2 mm thick; 5-very thick, more than 1.5



mm thick); 6) ground color of ventral hind wing (1-whitish gray; 2-whitish tan; 3-tan; 4-light brown); 7) degree of orange flush on disc of ventral forewing (1-no orange or ochre flush; 2-ochre flush; 3-orange-ochre; 4-mostly orange); 8) number of red lunules on ventral forewing margin (from 0 to 3); 9) number of red spots on dorsal forewing margin (red spot in cell 2A not counted) (from 0 to 4); 10) extent and thickness of dorsal hindwing marginal reddish band (1-absent; 2-only a few thin lunules; 3-longer but thin; 4-long and thick; 5-long and very thick); 11) extent of orange-ochre flush on dorsal forewing (1-absent; 2-several spots; 3-about 6 spots; 4-half of wing orange-ochre). Means for the first two characters are given (male mean above, female mean below).